On the Hawaiian Scallops of the Genus *Pecten* Muller (Pelecypoda)

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STRONGLY INEQUIVALVE SCALLOPS of the genus *Pecten* (s.str.) are represented in the western and central Pacific by relatively few living forms, most of which have widely separated distribution areas in Japanese and Australasian seas. Their fossil record and morphological affinities have suggested a rather unusual history of late Cenozoic dispersal and speciation, at least for the majority of Western Pacific species, which are discussed in a recent publication (Fleming, 1957). The most isolated of all Pacific scallops, recorded from the Hawaiian Islands as two new species, *Pecten waikikius* and *P. diomedeus,* by Dall, Bartsch, and Rehder (1938), were known only from left valves, and as a consequence their relationships have been difficult to interpret.

During the past few years, through the interest of Hawaiian conchologists, in particular of Mrs. M. E. King, extensive collections of offshore Mollusca have been dredged off the island of Oahu, including a number of specimens of both valves of a scallop. After examining the type specimens in the United States National Museum in October, 1960, the writer was able to study some of the new material during a short visit to Honolulu in November, 1960.

I am grateful to Dr. Yoshio Kondo, Bernice P. Bishop Museum, and to Dr. P. Burgess, Honolulu, for the opportunity to examine the specimens that are the subject of this paper. To Dr. F. Stearns MacNeil, United States Geological Survey, I am indebted for the reference to *Pecten byoritsuensis* Nomura and its record from Okinawa.

FAMILY PECTINIDAE

GENUS *Pecten* Muller, 1776

1776. *Zool. Danicae Prodromus:* 248.

Type species (by subsequent designation, Children, 1823): *Ostrea maxima* Linn.

The form described below is a typical member of the genus *Pecten* s. str., so closely similar to *Pecten jacobaeus* Linn. that it is here ranked as a subspecies of that species, which is a near relative of the type species of the genus.

The other form named from Hawaii (*Pecten diomedeus* Dall, Bartsch, and Rehder) is known from a unique valve and its relationships are thus uncertain.

Pecten jacobaeus (Linnaeus)

1758. *Ostrea jacobaea* Linn. Syst. nat. (ed. X): 696.

The races grouped in the polytypic species *Pecten jacobaeus* (see Fleming, 1957: 39) are characterised by their generally square-cut ribs, strong secondary radial threads on the surface of the main ribs, and well-developed concentric lamellae, which extend across both interspaces and ribs. The subspecies recognised to date are:

P. jacobaeus jacobaeus (Linn.). Mediterranean (Pliocene–Recent)
P. jacobaeus keppelianus Sow. Atlantic Islands (Recent)
P. jacobaeus byronensis Fleming. New South Wales (Recent)
P. jacobaeus toi Fleming. New Zealand (Pleistocene)
P. jacobaeus byoritsuensis Nomura. Formosa and Okinawa (Plio–Pleistocene)
P. jacobaeus meridionalis Tate. Tasmania–S.E. Australia (Pleistocene–Recent)
P. jacobaeus waikikius Dall, Bartsch, and Rehder. Hawaii (Recent)

Two other groups of far-flung populations related to *P. jacobaeus* have been grouped under different polytypic species, *Pecten modestus* Reeve (5 subspecies) and *Pecten maximus* (Linn.) (3 subspecies), because each seems to have had a separate history and to have retained a morphological unity since it separated from the *jacobaeus* stock, probably in the earliest Pliocene. As already hinted, however (Fleming,

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1957: 25), these species could be united into a single polytypic species if one were willing to attribute certain morphological resemblances to homeomorphy. The subspecies described below falls easily into the formenkreis of *jacobaeus,* which is known elsewhere in the North Pacific, yet it has some features in common with races of *maximus* (Atlantic–South Africa). Economy of hypothesis demands that these features be attributed to homeomorphy.

Pecten jacobaeus waikikius Dall, Bartsch, and Rehder

Fig. 1, *1–4*

1938. *Pecten waikikius.* B. P. Bishop Mus. Bull. 153: 95, pl. 24, figs. 5–6.

DIAGNOSIS: A small subspecies of *P. jacobaeus* distinguished from all other subspecies by the following combination of characters: extreme inflation of right valve, high swollen beaks, subangular-to-rounded primary ribs, secondary radial threads on both ribs and interspaces, crossed by concentric lamellae; left valve concave, with an asymmetrically raised adductor muscle scar.

Right Valve: Small, up to 52.5 mm long; length/height ratio 89.3, 89.5; beaks high and swollen; inflation 43.8 to 44.2% of length; ribs 17 or 18.

Sculpture: Ribs well defined but becoming more rounded towards the ventral margin than in most subspecies; interspaces about half their width. Rib summits on disc bearing rounded, secondary radial threads, somewhat irregular in strength and spacing, increasing by bifurcation from about 4 at 15 mm from beak to 6 or 8 at ventral margin. Flank ribs narrower, generally with about 2 secondary threads. Interspaces between ribs often with a single median secondary thread. Concentric lamellae, regularly spaced, first developed 12 mm from beak, crossing ribs, secondary ribs and interspaces alike. Ears with up to 5 radial threads, crossed by incremental lamellae. Colour, white.

Left Valve: (See Dall et al. 1938: 95). Strongly concave (more than 15% of length). Rib interspaces sometimes with up to 3 secondary grooves (corresponding with right valve threads) and ribs generally weakly grooved (corresponding with right valve interspace thread). Ears mostly with 2–5 weak radiating threads. Adductor muscle scar set on a thickened callus bounded in front by a linear ridge bisecting the beak angle. External colour, pale pink with subdued reddish flashes; interior, white.

Variation: The sample seen (5 right and 11 left valves) is remarkably uniform in shape and sculpture. A few right valves lack intercostal threads and a few left valves lack costal grooves. Auricular ribs are absent in two specimens.

LOCALITIES: Dall, Bartsch, and Rehder recorded left valves from off Waikiki, Oahu (type), off northeast Hawaii, and off Mala Bay, Maui. The new material is from off Keehi Lagoon, including the explosive anchorage area, Oahu, off Pekai Bay, and 1½ miles off Sand Island, Oahu. The depths range from 4–8 to 90–105 fathoms, but all specimens are single valves except a juvenile in the collection of Dr. P. Burgess, which was collected alive in 25 fathoms off Honolulu Harbor.

AFFINITIES: *P. j. waikikius* differs from *jacobaeus* s.str. and from the subspecies *keppelianius, byronensis, byoritsuensis,* and *meridionalis* in its high beak and inflation, strongly concave left valve, and distinctive left adductor scar. In sculpture it most closely resembles the ornamented phase of the extinct New Zealand Pleistocene form *P. j. toi,* but the latter is larger (up to 131 mm long), less inflated (29.5% compared with 44%), has a normal muscle scar, and is diphasic. In its rounded ribs, *P. j. waikikius* approaches subspecies of *P. maximus,* but this resemblance is probably homeomorphy.

In studying the relationships between different living and extinct populations of Pacific *Pecten,* the writer was led to the conclusion that members of the *jacobaeus* group were capable of hybridising with members of the *benedictus* group, when they came into geographical proximity, despite the evidence that the two groups had long been differentiated in the Mediterranean and had maintained themselves as distinct for most of Upper Tertiary time. For this reason, the subgenus *Oppenheimopecten* von Teppner, 1922, proposed for *Pecten subbenedictus* Fontannes, cannot be maintained. A member of the *benedictus* group, *P. benedictus excavatus* Anton (of authors, =*sinensis* Sowerby) lives in the China Sea, Formosa, and Japan, is

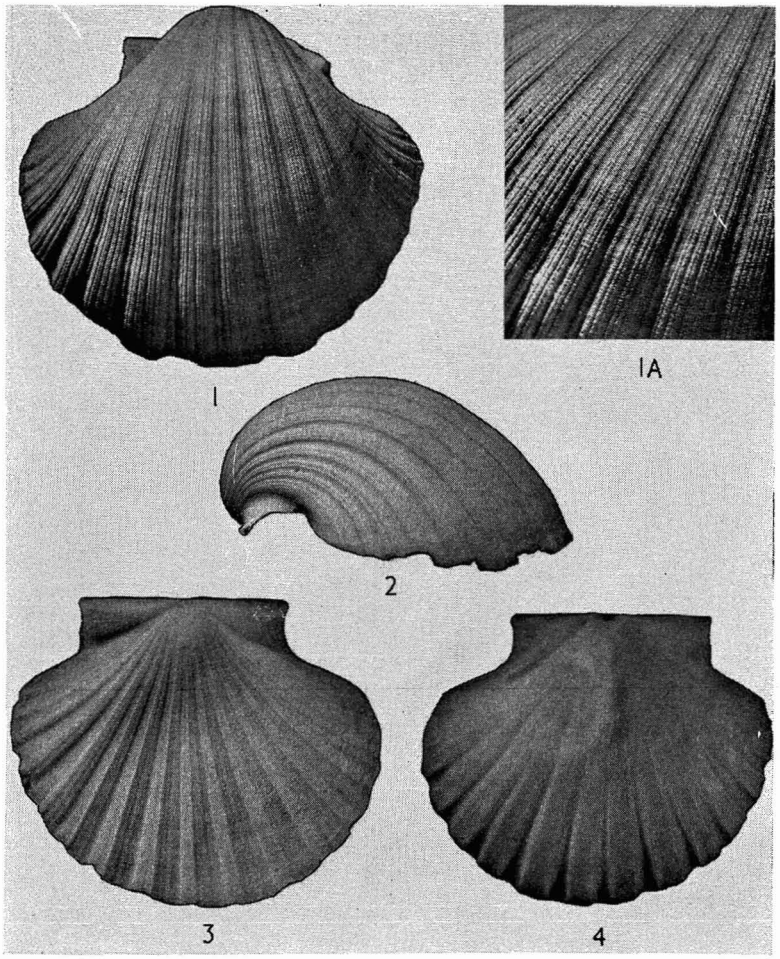

FIG. 1. *Pecten jacobaeus waikikius* Dall, Bartsch, and Rehder. Taken off Keehi Lagoon, Oahu, Hawaii, explosives anchorage area, 42–58 fathoms (Kirg Dredging Exped. Stn. 236, Aug. 1959). *1, 2,* Right valve, lateral and posterior views, × 1. *1A,* Detail of sculpture, right valve, × 1.5. *3, 4,* Left valve, exterior and interior views, × 1. Photograph, S. N. Beatus.

present at the Philippine Islands as dead valves (U. S. Nat. Mus., Bur. Fisheries Sta. 5162, 230 fathoms off Sanga Sanga Island), and perhaps formerly ranged far enough east to influence the Hawaiian population. It is even possible, as noted below, that a form of *benedictus* still lives at Hawaii. The characters of *waikikius* that could be attributed to interbreeding with a *benedictus* population are its extreme inflation, concave left valve, and rounded ribs. The peculiar adductor muscle scar of *waikikius* resembles that of a specimen of *sinensis* from Japan, but this character probably has a functional relationship to the extreme inflation of the right valve and is not necessarily an indication of close affinity.

Pecten (*? benedictus*) *diomedeus* Dall, Bartsch and Rehder

1938. *Pecten diomedeus,* B. P. Bishop Mus. Bull. 153: 96, pl. 24, figs. 7–8.

1957. *Pecten* (*? benedictus*) *diomedeus* Dall, Bartsch and Rehder; Fleming, N. Z. Geol. Surv. Pal. Bull. 26: 9.

This species is still known only from the type, a left valve differing from those of *waikikius* in being much less concave, and in its lack of auricular radial threads, in its ill-defined muscle scar, and in its lower ribs.

Examination of the holotype confirmed the impression that led to classification under *benedictus* (Fleming, 1957), and the uniformity of the *waikikius* sample now available strengthens the case for its specific distinction. This will not be certain, however, until right valves are obtained, since left valve concavity (and thus probably the nature of the adductor scar) are known to vary markedly in some *Pecten* populations (cf Fleming, 1957: 47) and auricular ribs are obsolete in some specimens of *waikikius*.

BIOGEOGRAPHY OF PACIFIC *Pecten*

In the light of later discoveries, the hypothesis that several species groups of *Pecten*, originating in other regions, colonised the Pacific in late Cenozoic times (Fleming, 1957: 23–25), is here recapitulated.

Of the several groups that entered the western Pacific, only one, now represented by the Japanese *Pecten albicans* Schroeter, shows relationships with America, where its extinct relations occur in the Miocene and Pliocene. Recently, however, Kanno (1960: 220) reported a poorly preserved shell close to *P. albicans* from the upper Oligocene of Japan. If this relationship were confirmed, the dispersal of the *albicans-aletes* group may have been from west to east, and not the reverse, as Grant and Gale (1931) postulated, but the matter must be left open at present.

Early members of the *jacobaeus* group had entered the Indian Ocean by the Miocene, and were represented there by a group of forms centred on *P. vasseli* Fuchs. Pliocene dispersals of members of the same group led to the widespread polytypic species *P. maximus* (northern Europe, with a representative in South Africa) and *P. modestus* (Mediterranean, Indian Ocean, and New Zealand). *P. jacobaeus* first appeared in the Mediterranean at the very beginning of the Pliocene, and by an unknown route (since it is not recorded as a fossil at intermediate localites) reached New Zealand (*toi*, Pleistocene), New South Wales (*byronensis*, Recent), Tasmania and southeast Australia (*meridionalis*, Pleistocene-Recent), Formosa and the Ryukyu Islands (*byoritsuensis*, Plio-Pleistocene), and Hawaii (*waikikius*, Recent). The earliest dates given in literature for these scallops in the Pacific is Pliocene, but downward revision of the Plio-Pleistocene boundary may eventually make them all Pleistocene. Some of the derivative races closely resemble the Mediterranean *jacobaeus*, but others have diverged in various ways. On the west side of the Tasman Sea, *P. j. meridionalis* has diverged in rib profile. In New Zealand a well-documented succession of Pleistocene populations suggests that the Recent species *P. novaezelandiae* was derived by loss of secondary sculpture from *P. jacobaeus toi*, and that the Kermadec Islands were colonised at an intermediate date in this Pleistocene history to produce *P. novaezelandiae raoulensis* Powell (1958).[2] It seems possible that the Formosa race *byoritsuensis* similarly gave rise to the smooth form *naganumanus* by loss of secondary sculpture, but this suggestion is not known to be supported by a stratigraphic sequence and the two occur together in Formosa (Nomura, 1933).[3] Other populations have retained the distinctive sculpture of *jacobaeus*, for instance *byronensis* in northern New South Wales and *waikikius* in Hawaii.

By a similar process of late Cenozoic range expansion by uncertain routes from the Mediterranean to the Pacific and subsequent disruption into isolated populations, the *benedictus* group of *Pecten* has reached the Red Sea (*erythraensis* Sow., Pliocene-Recent), New Zealand (several Pleistocene forms), Australia (*fumatus* and *albus*), the Philippine and China seas (*excavatus* of recent authors = *sinensis*), and perhaps Honolulu (*diomedeus*). Races of *benedictus* are more conservative than the *jacobaeus* group and are still quite close-knit in morphology.

The zoogeographic history of *Pecten* in the Indo-Pacific has some analogies with that of

[2] Wrongly shown as a member of the *benedictus* group in Fleming, 1957: fig. 3, but correctly classified in fig. 1. Originally described as *Pecten raoulensis* Powell.

[3] Nomura's record of *P. naganumanus* Yokoyama from Miocene of the Philippines is not supported by the reference to Dickerson (1922) that he cites.

Indo-Pacific Strombidae summarised by Abbot (1960: 842). Whereas *Strombus* first appeared in the early Miocene of the Tethys Sea, the groups of *Pecten* here considered arose in the Mediterranean basin and only later spread east into the Indo-Pacific. While tropical *Strombus* spread widely during the Pliocene, *Pecten,* preferring cooler seas, continued its spread in the early Pleistocene, when intermittent cool temperatures must have been more favourable than those of warmer Pliocene seas. As in *Strombus,* there was a shrinkage of ranges some time during the Pleistocene, so that the present distribution areas of *Pecten* subspecies are as strikingly discontinuous as are those of some subspecies of *Strombus.* Further discoveries of fossil or living populations in the Indian and Pacific oceans and the intervening archipelagos are likely to bridge the notable gaps in the known distribution of *Pecten* along the presumptive dispersal routes from the Red Sea to New Zealand, Japan, and Hawaii.

SUMMARY

The right valve of a rare Hawaiian scallop, named on the basis of left valves, is described and figured for the first time, and classed as a subspecies of *Pecten jacobaeus* (Linn.). Its place in the biogeographic history of the genus *Pecten* is discussed.

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